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Using plant, microbe and soil fauna traits to improve the predictive power of biogeochemical models

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Abstract

1. Process-based models describing biogeochemical cycling are crucial tools to understanding long-term nutrient dynamics, especially in the context of perturbations, such as climate and land-use change. Such models must effectively synthesise ecological processes and properties. For example, in terrestrial ecosystems, plants are the primary source of bioavailable carbon, but turnover rates of essential nutrients are contingent on interactions between plants and soil biota. Yet, biogeochemical models have traditionally considered plant and soil communities in broad terms. The next generation of models must consider how shifts in their diversity and composition affect ecosystem processes.
2. One promising approach to synthesise plant and soil biodiversity and their interactions into models is to consider their diversity from a functional trait perspective. Plant traits, which include heritable chemical, physical, morphological and phenological characteristics, are increasingly being used to predict ecosystem processes at a range of scales, and to interpret biodiversity-ecosystem function relationships. There is also emerging evidence that the traits of soil microbial and faunal communities can be correlated with ecosystem functions such as decomposition, nutrient cycling and greenhouse gas production.
3. Here, we draw on recent advances in measuring and using traits of different biota to predict ecosystem processes, and provide a new perspective as to how biotic traits can be integrated into biogeochemical models. We first describe an explicit trait-based model framework that operates at small scales and uses direct measurements of ecosystem properties; second, an integrated approach that operates at medium scales and includes interactions between biogeochemical cycling and soil food webs; and third, an implicit trait-based model framework that associates soil microbial and faunal functional groups with plant functional groups, and operates at the Earth-system level. In each of these models we identify

opportunities for inclusion of traits from all three groups to reduce model uncertainty and improve understanding of biogeochemical cycles.

4. These model frameworks will generate improved predictive capacity of how changes in biodiversity regulate biogeochemical cycles in terrestrial ecosystems. Further, they will assist in developing a new generation of process-based models that include plant, microbial and faunal traits and facilitate dialogue between empirical researchers and modellers.

1. Introduction

Recent improvements in computational power and co-ordinated research efforts into modelling ecosystem processes have advanced our understanding of biogeochemical cycles. However, a better understanding of the interactions between plants, microbes and animals is crucial to reduce uncertainty in carbon (C) cycling and the modelling of biogeochemical processes. Important aspects of these cycles include C turnover times (He *et al.* 2016), soil organic matter dynamics (Cotrufo *et al.* 2015), and soil carbon sink strength under a range of climate scenarios (Sofi *et al.* 2016). This will help address pressing challenges such as soil C loss and food security (Lehmann & Kleber 2015). However, there is a gap between the requirements of modellers and the empirical data produced through experimental research. Empirical data related to the functional role of organisms is needed to parameterise models under a range of spatial and temporal scales, ecosystem types and abiotic conditions. The consideration of functional traits promises to generate data that can help inform biogeochemical models (Violle *et al.* 2007; Moretti *et al.* 2017). Functional traits are heritable, morphological, physiological or phenological attributes of organisms that affect their growth, survival or reproduction, and thus, indirectly, fitness (Reich 2014). Many traits are commonly categorised as 'effect traits' and/or 'response traits'. Effect traits determine the effect of the organism on ecosystem processes, while response traits are characteristics that change in response to an external driver such as climate (Lavorel & Garnier 2002). Many traits may be both effect and response traits. Using functional effect traits instead of traditional diversity measures can generate more meaningful model predictions, because traits can offer mechanistic insight into the link between organisms and ecosystem function (Díaz *et al.* 2004; De Deyn, Cornelissen & Bardgett 2008; Faucon, Houben & Lambers 2017).

Traits have been widely used to predict how organisms influence ecosystem functioning, with a large focus on plant traits (Lavorel & Garnier 2002; Faucon, Houben & Lambers 2017). For

example, in tropical forests, stoichiometric traits of the tree canopy are strongly linked with nutrient cycling rates (Asner *et al.* 2015), while at local scales, physical and chemical traits of leaves and roots can affect soil C storage (De Deyn, Cornelissen & Bardgett 2008) and decomposition (Carrillo *et al.* 2017; Martin, Newton & Bullock 2017). One key advantage is that traits do not use taxonomy or numbers of species to infer function, which has previously been criticised (see the diversity-stability debate; McCann 2000). The intense focus on plant traits has resulted in the discovery of resource-use and performance related strategies. For example, the 'leaf economics spectrum' uses three plant traits (leaf nitrogen content, specific leaf area and leaf lifespan) to describe a continuum ranging from 'fast' to 'slow' growing species that affects ecosystem functioning (Wright *et al.* 2004). The principles employed in this approach may also apply to microbes and fauna, and literature is beginning to emerge on this theme (Allison 2012; Krause *et al.* 2014; Aguilar-Trigueros *et al.* 2015).

Soil microbes and fauna are key drivers of ecosystem processes, and contribute to ecosystem stability. However, frameworks to capture trait syndromes for soil organisms are in their infancy. Given the importance of soil microbes and fauna for biogeochemical cycles (Carrillo, Ball, Bradford, Jordan & Molina 2011; de Vries *et al.* 2013; Kardol, Throop, Adkins & de Graaff 2016), this represents a major hurdle when incorporating soil microbial and faunal traits into C and biogeochemical models. Furthermore, modelling ecosystem processes requires that traits must be constrained into the most parsimonious set of descriptors, so as not to overfit the model. Taking lessons learned from plant trait literature, it may be possible to identify microbial and faunal characteristics that are quantitatively linked to ecosystem processes to improve model parameterisation without exhaustive screening (Díaz *et al.* 2016; Kardol, Throop, Adkins & de Graaff 2016).

Soil biogeochemical models have long been used to describe the processes of C and elemental cycling in soil, but plants and microbes, two of the key drivers of these processes, are typically

included only in reductionistic terms because of the difficulty of accurately characterising these groups of organisms (Wieder, Grandy, Kallenbach, Taylor & Bonan 2015). The increasing rate of collection of new data on plants, as well as soil microbes and fauna, offers an opportunity to build on the advances made by previous models (e.g., CENTURY: Parton, Schimel, Ojima & Cole 1994; DAYCENT: (Parton, Hartman, Ojima & Schimel 1998); TEM: (Zhuang *et al.* 2011); CLM4: (Koven *et al.* 2013). Soil fauna have been included in biogeochemical models in broad terms, such as nematode and microarthropod biomass C (Grandy, Wieder, Wickings & Kyker-Snowman 2016; George *et al.* 2017). Increasingly, more nuanced models are possible due to better understanding of the role of faunal groups and availability of more comprehensive data on traits of these groups at different spatial and temporal scales. Evidence from soil food web models indicates that inclusion of plant, microbial and soil faunal traits and their interactions is imperative to improve the predictive power of biogeochemical models (Allison 2012; Wieder, Bonan & Allison 2013; Filser *et al.* 2016; Faucon, Houben & Lambers 2017; Funk *et al.* 2017). To move forward, we propose that gaps in knowledge of measuring and understanding functional traits must be addressed and general principles must be identified.

Here we propose frameworks to incorporate plant, microbial and soil faunal traits in predictive models to better simulate the dynamics of biogeochemical cycles in terrestrial ecosystems. We use the decomposition of soil organic matter (SOM) as an example because it is a key driver of the terrestrial C cycle, and will likely be affected by global climate change (Davidson & Janssens 2006). Moreover, there are well-established mechanisms to suggest that plants, microbes and soil fauna interact in context-specific ways to influence decomposition (Swift, Heal & Anderson 1979; Allison 2012; Filser *et al.* 2016), making them ideal candidates for inclusion in such models. First, we highlight knowledge gaps in the traits framework and the potential for sets of traits (e.g., stoichiometry, resource capture strategy) between plants, microbes and soil fauna to correlate.

Second, we seek to bridge the gap between modellers and experimental ecologists by outlining what types of data are feasible to collect and useful as inputs to models (Table 1). Finally, we discuss the uses and limitations of three types of commonly used models (explicit, integrated and implicit) and describe why incorporating traits from plants, microbes and fauna will help improve the predictive power of these models.

2. The potential for using traits to describe biogeochemical processes

Plant traits have been used extensively to understand the links between plant communities, ecosystem processes and environmental change (Funk *et al.* 2017). This approach has several advantages, including cost and time effectiveness, and the ability to scale trait distributions from the individual to the landscape level. For example, plant traits change predictably across climatic envelopes (Díaz *et al.* 2004), elevational gradients (Read, Moorhead, Swenson, Bailey & Sanders 2014) and management regimes (de Vries *et al.* 2012). In fact, exploring plant traits across chronosequences (i.e., space-for-time substitution, as seen across successional gradients; Walker, Wardle, Bardgett & Clarkson 2010) has allowed for a better understanding of how traits can predict ecosystem processes at both temporal and spatial scales (Wardle, Walker & Bardgett 2004; Kumordzi *et al.* 2015). Arguably the most important aspect of functional traits is the strong links identified with biogeochemical processes. Soil C storage across biomes can be influenced by traits including leaf nitrogen (N) content and relative growth rate (De Deyn, Cornelissen & Bardgett 2008), while similar traits drive decomposition (Carrillo *et al.* 2017). As such, aboveground plant traits have typically been considered to fall on a spectrum between those promoting fast and slow cycling of nutrients (analogous to r- and k-strategists in microbial commnuities), with plants with 'slow' traits promoting the formation of more stable SOM than plants with 'fast' traits (De Deyn, Cornelissen & Bardgett 2008). Extending this paradigm to microbial and faunal groups may be

128 possible. For example, increasing leaf N is likely to increase palatability for soil fauna and microbes,
129 and so N-rich leaves are likely to be preferentially decomposed by highly exploitative r-selected
130 microbial and faunal groups. This suggests that plant, microbe and soil fauna traits might align in
131 predictable ways (Box 1). However, the fast-slow decomposition paradigm has recently been
132 challenged, with greater emphasis on the accessibility of SOM as opposed to the chemical
133 composition (Lehmann & Kleber 2015). Therefore, relative resource use rates of the three groups
134 may have important connotations for whether decomposable SOM is incorporated into microbial or
135 faunal biomass.
136 Recent literature has identified the most important microbial traits that can predict or be
137 predicted by ecological processes (Aguilar-Trigueros *et al.* 2015; Treseder & Lennon 2015); (Table
138 1). A key distinction has been drawn between free-living microbes and those dependent on host
139 species. It is assumed that responses of the free-living species are more environmentally mediated,
140 while microbes dependent on host species (e.g., mycorrhizal fungi, rhizobia) may respond primarily
141 to cues from the host plant (Friesen *et al.* 2011; Crowther *et al.* 2014). Fungi can have mutualistic,
142 pathogenic and saprotrophic life cycles, with accompanying variation in morphology, chemistry and
143 resource use efficiency (Aguilar-Trigueros *et al.* 2015). This variation creates a major hurdle for
144 those trying to find unifying principles across microbial groups. Additionally, the assembly of a free-
145 living fungal community is largely based on environmental gradients, with resource availability
146 being a key determinant. This could mean a decoupling of plant and microbial community assembly
147 processes under environmental stress (Box 1). Accordingly, Crowther *et al.* (2014) presented a
148 continuum based on resource use, with highly competitive fungal taxa occurring in resource-rich,
149 low-stress conditions, and stress-tolerant taxa occurring when resources are scarce or conditions are
150 harsh. However, the problem herein is that many of these spectra account for 'response traits' not
151 'effect traits', and are therefore potentially too variable or context-specific for models that aim to

predict ecosystem function. Further, resource availability for plants may not match resource availability for fungi, partly because of more conservative resource use, partly because of differing stoichiometric requirements (de Vries et al. 2012). A similar problem is likely to apply to bacterial distributions (Martiny, Jones, Lennon & Martiny 2015). Knowledge of abundances, or presence/absence of certain important bacterial groups with specific functional traits, such as methane oxidising bacteria and phosphate solubilising bacteria, is likely to be the most effective way of including bacteria in models, given the problems with dormancy (Fierer 2017) and defining bacterial species (Caro-Quintero & Konstantinidis 2012).

Trait classifications for soil fauna are beginning to emerge. For example, Pey *et al.* (2014) suggest 20 trait measurements in five broad categories (morphology, physiology, feeding, life history, and behaviour) that can be utilised across invertebrates. Moretti *et al.* (2017) proposed standardized measurements for 29 traits known to be sensitive to global stressors and to affect ecosystem processes (Table 1). As fauna tend to be mobile, community weighted mean (CWM) traits may be useful to predict ecosystem processes. Traits such as feeding habit or body size are particularly responsive to environmental changes (Farská, Prejzková & Rusek 2014), and functional diversity metrics based on these traits are effective in describing decomposition (Milcu & Manning 2011). We need to identify traits that can encompass the structure of the food web to be able to include several trophic groups and their interactions. Taken together, plant, microbial and soil faunal traits offer a way to improve the accuracy of biogeochemical models, but for the latter two groups, a crucial first step is to disentangle the role of response and effect traits.

There are some issues concerning the integration of plant, microbe and soil fauna traits into biogeochemical models. One major consideration is the turnover rate of microbial and faunal communities. In contrast to plants, microbes and soil fauna often have a high turnover rate, and they can adapt their metabolism or feeding strategies quickly to new conditions. Additionally, faunal

composition may rapidly change. Resource use and turnover are likely useful traits to describe these groups, because they correlate directly with biogeochemical processes, with relative biomass of each group dictating the importance of that group in the system (Crowther *et al.* 2014; Fierer 2017). Further, we need to find a set of easily measurable descriptors for traits across all three groups that will describe key soil functions, such as decomposition, robustly across a range of conditions and biomes. There are potential shortcuts using prior knowledge obtained from the plant trait literature. The biomass ratio hypothesis states that the influence of an individual or species on a function is proportionate to its biomass in the ecosystem (Grime 1998). Therefore, it is possible that rather than measuring complex, continuous traits, categorical data such as feeding group could be constrained to an ordinal scale and weighted by abundance (i.e., CWM) (Fierer *et al.* 2014). Assessing activity of the whole community could offer a solution, and there are numerous methods, including the measurement of enzyme activities involved in decomposition and respiration rates, to achieve this.

We also need to include interactions between plants, microbes and soil fauna into models because these interactions can have large effects on C fluxes (Johnson *et al.* 2005; Kanters, Anderson & Johnson 2015). Of primary consideration is the level of organization within soil food web communities. There are extensive data regarding the assembly of soil food webs associated with particular plant species that can inform explicit models (Yen *et al.* 2016), but such data needs to demonstrate quantitative correlations with biogeochemical cycling. However, it remains uncertain as to when, how and why these associations form and deteriorate across larger scales (Nilsson & McCann 2016). Furthermore, transfers of C and N between plants, microbes and soil fauna are relatively well characterized and have been used in models examining food web energy flows (Pausch *et al.* 2016). The next step is to apply this knowledge to test broader hypotheses (Table 2). Ideally, we need to know whether plant, microbial and faunal groups respond in the same direction under a given scenario. For example, under a drought event, plants may temporarily stop

200 photosynthesizing, thereby reducing root exudation, which leads to a reduction in bacterial biomass
201 and thereby soil fauna (Box 1). There are likely to be other scenarios where one group can capitalize
202 on the decline of the others, and these scenarios are likely to be unpredictable and thus difficult to
203 include in models. Therefore, in order to create unifying principles across plants, microbes and soil
204 fauna, it is imperative to identify traits that have robust relationships with function (e.g., nutrient
205 requirements) and avoid highly plastic traits in order to be able to use them across large spatial scales
206 and contrasting environmental conditions.
207
208 **3. Incorporating a trait-based approach into biogeochemical models**
209 Models require several data formats, depending on their scope. For example, an explicit
210 decomposition model can use raw data from field experiments, such as CWM leaf traits or
211 abundance of soil fauna. Integrated and implicit models, however, may need data in the form of
212 correlation coefficients between the drivers of decomposition, as well as reasonable *a priori*
213 parameter values. These requirements make it difficult to acquire appropriate data for such models.
214 For the microbial and faunal traits, an ideal starting point would be to assemble databases of traits
215 across ecosystems, climates and land use types (Burkhardt *et al.* 2014) that resemble the TRY
216 database for plants (Kattge *et al.* 2011). However, as such databases are assembled for microbes and
217 soil fauna, caution must be taken to account for variability in the data that might be due to inherent
218 factors such as intraspecific variability, and the use of different methods to measure microbial and
219 faunal traits.
220 Recently, there has been considerable effort to develop working trait-based models, although
221 at the time of writing, models are yet to include all three taxonomic groups (i.e., plants, microbes
222 and fauna). For example, there are models based on plant community assembly (Xu, Medvigy,
223 Powers, Becknell & Guan 2016), microbial processes (Allison 2012; Wieder, Bonan & Allison

2013; Wieder, Grandy, Kallenbach & Bonan 2014; Hararuk, Smith & Luo 2015), and certain faunal groups (van Bodegom, Douma & Verheijen 2014; Yen *et al.* 2016). However, model generalisation remains challenging due to their complexity, limited data availability and scalability. Uncertainty in modelling biogeochemical processes has two components, namely that arising from detail and precision in the data, and from the model itself (Keenan, Carbone, Reichstein & Richardson 2011). Quantification of data and model uncertainties is therefore imperative to determine the accuracy and interpretability of model predictions. Regardless of the type of model, it is important that they are continually tested using appropriate data, and that they are used in ecosystems where they have been developed and validated. The evaluation of a process-based model depends strictly on the quality, type and frequency of the measured values used to test the model.

In order to construct an effective model for linking biological communities with decomposition rates across multiple trophic levels, there is a need for robust trait data that incorporates spatial and temporal elements. Although there have been numerous case studies exploring individual response or effect traits, little is known about interactions between traits (e.g., trade-off), association between response and effect traits across and within trophic levels, and variation of traits within and between species across space and time (i.e., trait plasticity) (Ackerly & Cornwell 2007; Krause *et al.* 2014). Belowground biotic traits, such as specific root length or microbial growth efficiency, have not been properly quantified in terms of their optima, intra- and interspecific variation, trade-offs, and functionality (Bardgett 2017; Laliberté 2017). Quantifying which traits affect which processes and how such relationships vary across space and time is vital for process-based models. As a first step, well-coordinated data collection efforts are needed on trait correlations along trophic and environmental gradients (Wieder *et al.* 2015). To achieve this, there is an urgent need to identify traits that are relatively easy to measure yet informative so that they strongly interact with environmental gradients and/or are crucial for fitness (McGill, Enquist, Weiher & Westoby 2006)

(Table 1). Once links between traits and ecosystem function have been established across contrasting spatial and temporal scales, it will be important to evaluate if their inclusion improves the predictive power of models.

Types of models that will benefit from incorporating plant, microbial and soil faunal traits

Depending on the complexity and the predictive power needed, microbes and soil fauna can be either explicitly or implicitly represented in an ecosystem model (Figure 1). Below we outline three possible frameworks to incorporate belowground organism traits and processes in biogeochemical models: 1) an explicit trait-based model framework that operates at the small scale (space or time, or both) and uses direct measurements of ecosystem properties 2) an integrated approach that operates at a medium scale and includes interactions between a model component on biogeochemical cycling and that on the soil food web, either of which could be populated with measured data; and 3) an implicit trait-based model framework that operates at a large scale (i.e., Earth system) and associates microbial and soil faunal functional groups with plant functional groups. To fit with the focus of this manuscript, we separated the models based on how microbes and soil fauna are represented in the models, as well as the spatial or temporal scale at which each model is best equipped to operate (Figure 1). The scope of this separation is to discuss possible frameworks to incorporate belowground traits into soil process based models. It should be noted that the classification system proposed here is not the only way such models can be grouped or defined.

Explicit models

Explicit models seek to parameterise relationships between variables, typically known as the dependent and independent variables. Such models in the context of biogeochemical cycling explicitly include microbial biomass. The goal of these models is to predict the dependent variable

(e.g., decomposition) (Parton, Schimel, Cole & Ojima 1987). Explicit trait-based models, such as those developed for the simulation of microbial communities (e.g., Allison 2012) and faunal communities (Filser *et al.* 2016), require extensive knowledge of the intra- and interspecific trait variation along environmental gradients and their effects on ecosystem pools and fluxes. Two major advantages of this approach are: (1) the explicit parameterization of traits allows for measured values as direct model input; and (2) complex interactions between organisms are allowed and may lead to emergent properties, such as top-down or bottom-up regulation of food web structure. For example, in Figure 1a, microbial communities could be represented by r-selected (R_{mic}) and K-selected (K_{mic}) groups, with R_{mic} defined by traits that exhibit fast-growing attributes that compete with plants for easily available nutrients, and K_{mic} as slow-growing, but able to utilize recalcitrant materials (e.g., Wieder *et al.* 2015). To simulate these processes, we need to determine the growth and nutrient uptake efficiencies of R_{mic} and K_{mic}, and the trait-function and trait-abiotic relationships. Further, the relationship between R_{mic} and K_{mic} and soil fauna (i.e., grazers, predators) will need to be better understood. This framework explicitly simulates trait trade-offs of different belowground biotic groups, which is useful for understanding fine-scale, non-linear system dynamics. Understanding of how belowground traits should be incorporated into the mathematical equations of such models has shown promising development (McCormack *et al.* 2017) (e.g., specific root length, Table 1). In addition, models incorporating this level of complexity may exhibit unrealistic simulation behaviours (e.g., Hararuk, Smith & Luo 2015). Explicit trait-based models will benefit from efforts that quantify how the traits of different biotic groups affect ecosystem processes across different ecosystems, which may be achieved through meta-analysis and enhancement of trait databases (Table 2; Funk *et al.* 2017).

Integrated models

296 Integrated models are a mix of measured and inferred variables. These process-based models have
297 been developed from an understanding of how soil is affected by its abiotic and biotic properties,
298 land management and climate (McGill 1981; Smith *et al.* 1998). This approach integrates
299 biogeochemical and soil food web (i.e., microbial and soil faunal interactions driven by inputs from
300 plants) models (see Table 2 for examples of potential research questions). Here, mass and C are
301 recycled in the former model, and plant, microbial and soil faunal functional traits affect the rate of
302 mass transfer as a consequence of simulation in the latter (Figure 1b). These two models operate at
303 different timescales and spatial resolutions, as the biogeochemical model does not directly simulate
304 population demography and community assembly. The level of complexity of the soil food web
305 model varies depending on the research question and data availability, with soil food webs either
306 condensed into a metric of biodiversity or explicitly represented by their respective plant, microbial
307 and soil faunal groups. A metric of community diversity could be calculated for the soil food web
308 model and used to modify the rate of decomposition in the biogeochemical model (dashed arrows in
309 Figure 1b). For this integrated model to work, however, connections on how soil food webs affect
310 elemental transfers, and how plant ecophysiology affects competition and demography must be
311 quantified. Additionally, the ability to track changes in vegetation functional trait composition
312 through time and space without tracking species composition along different trophic levels is
313 necessary.
314
315 *Implicit models*
316 Finally, implicit models are often used to attempt to predict functions or processes at the global scale.
317 Well-known examples of implicit models include the CENTURY model, which predicts soil C, N
318 and nutrient turnover based on SOM turnover and plant functional type (Parton, Schimel, Ojima &
319 Cole 1994). Implicit trait-based models (Figure 1c) incorporate belowground biotic traits by making

the assumptions that microbial and soil faunal functional traits have clear associations with plant functional traits, and their responses to environmental perturbations are similarly predictive (see Box 1; Table 2). Such an approach would allow Earth system models to maintain the basic structure of their simulation of decomposition. Implicit models assume that plant attributes exhibit top-down control on processes such as decomposition. Therefore, microbial and soil faunal groups are expected to be adapted to such controls. This means that relationships between diversity, disturbance and productivity are well established in a given location. Most of the existing land surface models operating at large spatiotemporal scales have adopted this approach (e.g., CLM: Yang et al., 2014; CABLE: Wang et al., 2010; O-CN: Zaehle & Friend, 2010).

While this approach enables Earth system simulations at coarse spatial resolutions, at the time of writing, such simulations cannot incorporate intraspecific trait variation of microbes and soil fauna and their potential consequences for ecosystem processes. The possibility that plant, microbial and faunal traits do not respond similarly to stress, and are not subject to the same spatial or temporal patterns, are also beyond the scope of the current models because of limitations in data (Box 1). One solution could be the integration of statistical tools such as Bayesian hierarchical modelling to estimate intraspecific trait variation and species interactions (Funk *et al.* 2017). However, this only provides a probabilistic estimate of the consequence of multiple ecosystem processes. Nevertheless, this approach represents a compromise among factors such as data availability, scalability and predictive power, and is practical based on existing Earth system models.

The way forward

Ultimately, without improved communication between those who collect empirical data and those who model biogeochemical cycles, efforts to close the knowledge gaps are doomed to fail. Here we suggest five important steps to unite research efforts:

1. **Determine standardised approaches to measure microbial and soil faunal traits.** Plant traits are typically easier to measure than microbe and soil fauna traits (Table 1), but this hurdle must be overcome in order to successfully populate models with traits from all three groups.
2. **Determine which plant, microbial and soil faunal traits are the best predictors**. Traits that are associated with resource economy and stoichiometry are strong contenders, but traits linked to morphology and longevity cannot be overlooked, as they potentially infer links with amount of resources added to the system and turnover rate (Table 1). This stage will require that models are run and their validity checked by comparing predicted outputs to real data.
3. **Acquire knowledge about the interactions between traits, between individuals (within and between taxonomic groups), and trade-offs that might affect the model's predictive ability**. For example, increasingly, alignment between mycorrhizal fungi and plant hosts are known and can be included in models. Including data on habitat filtering of various taxonomic groups from a trait based perspective would be extremely useful.
4. **Determine whether plant, microbe and fauna traits align in a predictable way, particularly in response to stress and trophic and environmental gradients**. Assessing the plasticity and inherent intraspecific variation of traits and also including "extended phenotypes" (e.g., pathogen susceptibility, rhizosphere community composition), as traits themselves would help achieve this goal.
5. **Determine how to generate the best data for the different model types (i.e., explicit, integrated, explicit).** This aim requires close dialogue between modellers and field ecologists to determine which questions can be answered using different models (Table 2).

More generally, when designing large scale or long-term empirical studies, we recommend including the expertise of a modeller, in order to ensure the data is appropriate for use in models. Only through integration of plant, microbial and soil faunal traits, as well as a more robust dialogue between modellers and empiricists, will the next generation of biogeochemical models more accurately represent Earth system processes.

Acknowledgements

ELF is supported by the NERC Soil Security Programme (NE/P013708/1); JRD and BGJ by the UK Biotechnology and Biological Sciences Research Council (BBSRC) (Grants BB/I009000/2 and BB/I009183/1). DJ receives partial support from the N8 AgriFood programme. This work was supported by a BBSRC International Partnering award (BB/L026759/1) to EB, DJ, RB and PS.

Figure 1.

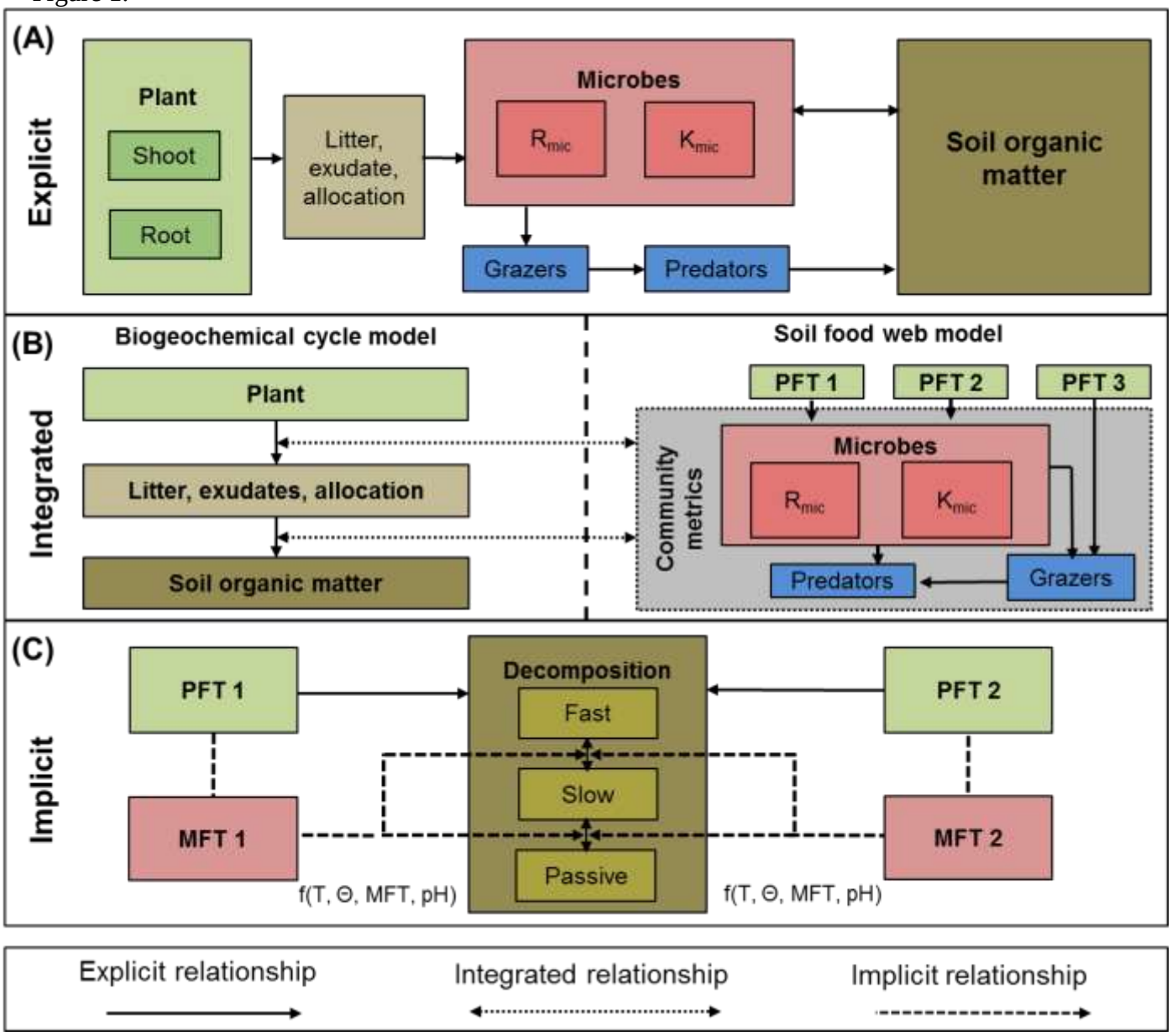

Figure 1. Three biodiversity-biogeochemical model types that could be developed to incorporate biotic traits of plants, microbes and soil fauna. A) An explicit small-scale trait model that simulates plant traits (e.g., root and shoot stoichiometry, quality) and microbial traits (e.g., r- versus K-selected, carbon use efficiency) and trade-offs, with the transfer of carbon between the soil food web (including trophic cascades) and soil biogeochemical cycling (e.g., decomposition) explicitly simulated. B) An integrated small-scale model through the connection of a biogeochemical model

and a soil food web model. Carbon moves through the biogeochemical model, whereas the soil food web model simulates functional trait attributes or community metrics of different plant functional types (PFT), r- and K-selected microbes and soil fauna such as grazers and predators. Such models only provide output to influence the rate of carbon movement in the biogeochemical model, here decomposition. C) An implicit large-scale model, with microbial functional types (MFT) coupled with PFT. Traits are used to parameterise the association and trade-offs among MFT and PFT. Therefore, the traditional decay rate constant for soil organic matter is replaced by MFT-specific functions that account for the size and type of the target MFT and abiotic factors (e.g., temperature, energy transfer, soil pH). Soil organic matter that is decomposed is partitioned into fast, slow and passively cycling pools to better account for variability in soil residency time. Scalability is enabled through this approach, making such models more useful for Earth system modelling. Boxes represent different physical and biological pools, and lines represent different coupling relationships (i.e., explicit, integrated, implicit).

Table 1. Hypothetical *a priori* usefulness and measurability of plant, microbial and faunal traits to our proposed explicit, integrated and implicit biogeochemical models. Note that the measurability designations of easy, medium and hard in this table are approximations and may vary across ecosystems and focal species.

Taxa	Trait	Measurability of trait			Usefulness for model			References
		Easy	Medium	Hard	Explicit model	Integrated model	Implicit model	
Plant	Morphology	Growth form Height Leaf area Rooting architecture		Root diameter Root area	✓			(Cornelissen *et al.* 2003)
	Longevity	Relative growth rate Life span Seed mass Seed number Seed bank longevity Dispersal			✓	✓	✓	
	Stoichiometry	Leaf/root C, N, P content/ratios			✓	✓	✓	
	Resource economy	Leaf dry matter Leaf toughness	Specific leaf area Photosynthetic/ respiration capacity Regulation of stomatal conductance (g_1)	Specific root length	✓	✓	✓	
Microbe	Morphology	**Fungi:** Hyphal exploration type **Bacteria:** Gram negative or Gram positive	**Fungi:** Mycelial architecture Hyphal length Maximal hyphal growth rate		✓			(Aguilar-Trigueros *et al.* 2015; Buchkowski, Bradford, Grandy, Schmitz & Wieder 2017)
	Longevity	**All:** Growth rate	**All:** Death rate Predation Competition		✓	✓		
	Stoichiometry		**All:** C:N:P ratios		✓		✓	

	Resource economy	**Fungi:** Hyphal diameter Chitin wall thickness Free-living to symbiotic **Bacteria:** Feeding substrate Substrate affinity Free-living to symbiotic	**Fungi:** Production of non-enzymatic substances (antibiotics) Enzyme activity **Bacteria:** C use efficiency Community dynamics		✓		
Fauna	Morphology	Mode of movement Aggregation /gregariousness				✓	(Pey *et al.* 2014)
	Longevity	Egg size Clutch size Age at maturity Population density	Growth rate Life span			✓	
	Stoichiometry	C:N:P ratios			✓		
	Resource economy	Feeding substrate	Activity time		✓		

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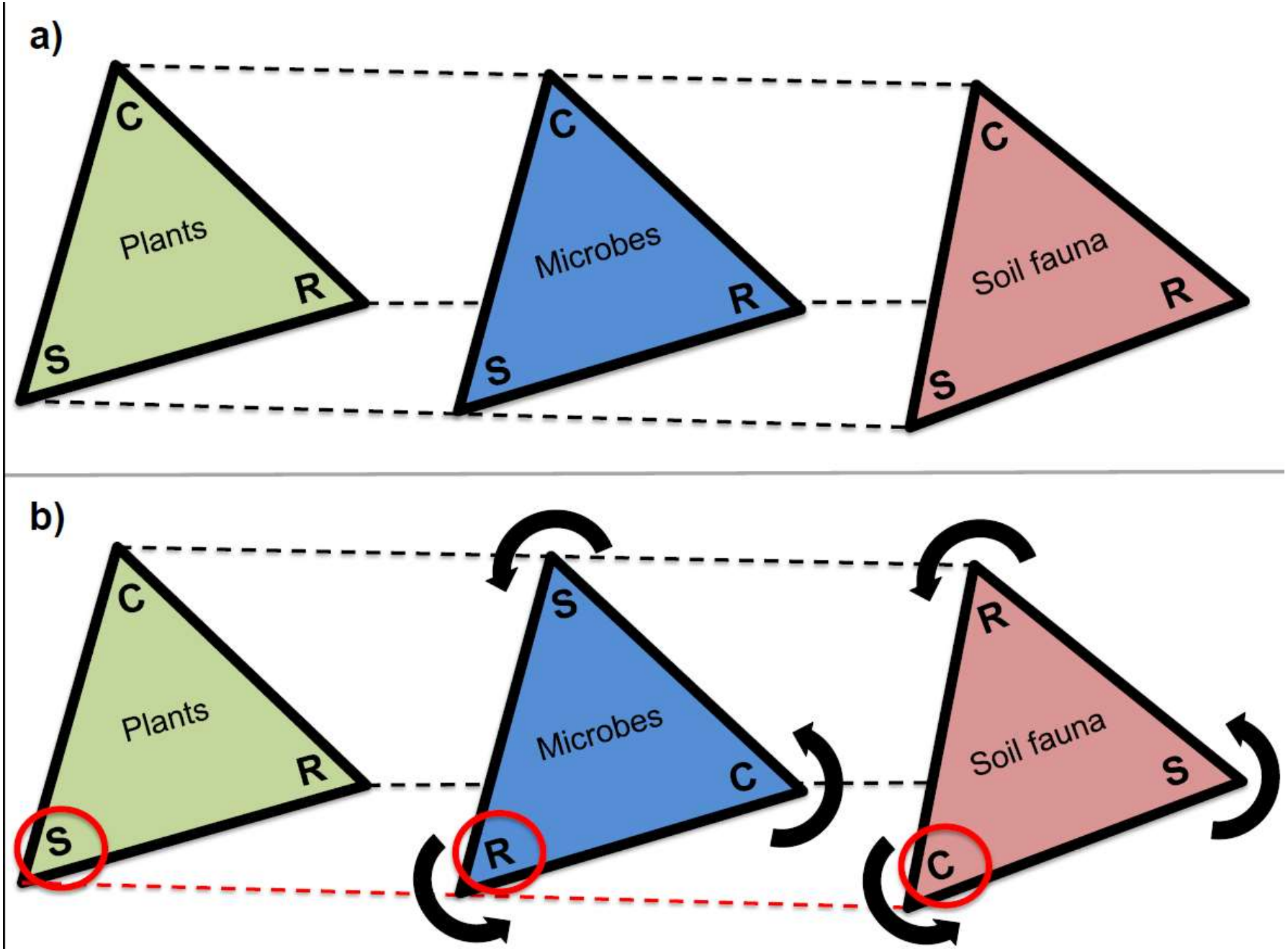
Table 2. Questions that can be addressed by different trait-based ecosystem models. Explicit, integrated and implicit models are best equipped to answer ecological questions across fine, medium and large spatial and/or temporal scales, respectively, and therefore the questions are organised to reflect this hierarchy.

Type of model	Potential questions
Explicit model	How can a particular trait be incorporated into an ecosystem model? How do different ecological strategies that are represented by different combinations of traits affect ecosystem fluxes and pools? What emergent processes arise from introducing complexity into soil C cycling?
Integrated model	How do alterations to the soil food web influence soil C storage? Is soil C storage differentially affected by 'top-down' vs. 'bottom-up' control of soil food webs? How does drought influence soil C storage? How does an increase in productivity change food webs? How does land management influence CO_2 emissions? How does earthworm invasion influence soil organic matter dynamics? How do changes in diversity affect soil organic matter composition?
Implicit model	What is the effect of land use or management change on soil C stock? How does spatial variation in the projected changes of climate drivers influence soil C storage? How does global warming affect soil C stocks?

Box 1. Connecting traits across groups: plants, microorganisms and animals

A number of paradigms have been proposed to classify organisms within groups according to their functional traits. For example, Grime (1977) proposed the competitor/stress tolerator/ruderal (C-S-R) framework to explain how plants with different traits adapt under different environments. Wright *et al.* (2004) built upon this concept, suggesting that plants can be globally classified along a spectrum from those that are fast growing and promote fast nutrient cycling, to those that grow more slowly and promote slower nutrient cycling, known as the 'leaf economics spectrum'. It would be desirable from a modelling perspective to align functional effect traits across plants, microbes and soil animals using one of these existing paradigms, but this presents challenges. Microbes have generally been classified along an r-selected to K-selected continuum, which has been the main framework for including microbes in models (Figure 1; Wieder *et al.* 2015). Further, soil animals exhibit 'behavioural traits' (Pey *et al.* 2014), adding additional complexity, and allowing them to readily move between resource patches. Attempting to create such frameworks for soil animals is still in its infancy, though recently there has been growing interest in attempting to describe the patterns (Grandy, Wieder, Wickings & Kyker-Snowman 2016). Certain links among groups of organisms are relatively well established, particularly between plants and microbes. For example, out of 30 commonly measured plant functional traits (Cornelissen *et al.* 2003), 14 have been identified as microbial mediated (Friesen *et al.* 2011). One way to further develop these known links is to consider a 'bottom up' scenario, where plants influence microbes, which influence fauna in a simple hierarchy. This is likely to select for different characteristics (i.e., different sectors of the C-S-R framework) for each group. For example, a stressed plant (S) is likely to offer an increased resource pool due to root sloughing and exudation, which would favour the ruderal-selected microbial community (R), which could offer opportunities for competitive groups of soil fauna (C). This is depicted in a conceptual diagram showing C-S-R triangles rotated accordingly across taxonomic groups (see inset a). Krause *et al.* (2014) adapted the

C-S-R framework to explain microbial community functional traits, arguing that microbial communities employ similar strategies to those used by plants. We suggest that on small or local scales, they often do not. This is because plants, microbes and animals operate at different spatial, temporal scales and resource requirements, and a catastrophic event for one group could lead to an opportunity for another (e.g., Birch 1958). Conversely, overall patterns of resource economy have been identified across larger landscape scales that indicate that there are general patterns that may align with management intensity or climate. Intensive management often increases nutrient availability, which selects for 'competitive' plant species (C) and bacterial-dominated food webs. Nutrient poor ecosystems select for stress-tolerant (S) species, which leads to fungal-dominance (de Vries *et al.* 2012; de Vries *et al.* 2013, see inset b). This may therefore be an appropriate assumption for larger scale implicit models, and thus plant functional type may be sufficient to infer the activity of the rest of the soil food web (but see van Bodegom *et al.* (2012)). Please note that the C-S-R framework highlighted here is only one possible scenario under which plant, microbial and soil faunal trait spectra may align. Alternative alignments of trait spectra between plants, microbes and soil fauna that could help inform the creation of models are certainly possible.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